# Allometry in the Bearded Dragon *Pogona barbata* (Sauria: Agamidae): Sex and Geographic Differences

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ABSTRACT

Allometry in size and shape between sexes was investigated in preserved Bearded Dragon *Pogona barbata* museum specimens. Measurements for snout-vent, head, leg and tail lengths were obtained from 236 individuals ranging from hatchlings to large adults. Juveniles and adults were sexed, and size at onset of maturity was determined. Geographic variation in *P. barbata* was also studied by comparing lizards from three regions in New South Wales (NSW), which differ in annual rainfall.

Relative to snout-vent length, head and leg lengths were in negative allometry in all specimens, and tail length was in positive allometry in juveniles, but negative in adults. Sexual dimorphism was evident in body size and shape. Males grew larger and reached maturity at larger sizes than females. While juvenile shape did not differ between the sexes, mature males had proportionately longer heads, legs and tails than adult females. This generalisation in sexual shape dimorphism did not hold true for animals from different NSW regions. Western males had proportionately longer legs and heads than western females, but relative tail lengths were not significantly different. Sexual dimorphism in body shape was not seen in the central animal group. In the east, heads and tails were longer in males than in females. Both sexes showed lower relative head and leg lengths in more arid regions. We suggest that a combination of genetic drift and phenotypic responses are likely causes of these variations.

Key words: *Pogona barbata*, allometry, sexual dimorphism, geographic variation, morphology

## Introduction

Growth, and ultimately body size, are among the most important life history traits that affect the physiology and ecology of an organism (Gould 1966; Cyr and Pace 1993). An important aspect of growth is the proportional relationship of the various body parts to that of the whole organism (Weatherly and Gill 1987). This relationship follows an orderly system, where relative growth rates of different body parts vary among each other, leading to changes in body shape. Certain changes in body shape result through natural selection because they are mechanically or physiologically required by size increase (Gould 1966).

Huxley (1932) first demonstrated a mathematical relationship between the relative size of an organ and the absolute size of the organism. He described that relationship, known as allometry, in terms of the simple formula $y = ax^b$, where x is a measure of the size of the animal, y is the size of the differentially growing organ and b is the growth coefficient or allometric coefficient. The allometric coefficient is therefore a measure of the direction and the extent of growth related change in the organ under investigation. For example, a coefficient greater than 1 for leg length states that relative leg length increases with increasing body length. A special form of allometry is isometry, where the coefficient equals one and where there is no change in proportion with increasing body size.

Sexual dimorphism of body size and shape is common in many animals, with females generally the larger sex among invertebrates and poikilothermic vertebrates, while males predominantly grow larger among birds and mammals (Fairbairn 1997). Sexual size dimorphism is relatively common in reptiles (Patchell and Shine 1986). Studies of sexual dimorphism in reptiles include those on snakes (eg. Shine *et al.* 1998), crocodilians (Webb and Messel 1978) and various lizards (Schoener 1967; Fitch 1981; Patchell and Shine 1986). Apart from gender, variation in environmental factors may also be responsible for size and shape differences among populations.

In this study, we investigate allometry and sexual dimorphism in the agamid Bearded Dragon *Pogona barbata* (Cuvier 1829). Some aspects of the species' biology have been well studied (see below). However, growth-related studies have largely been ignored with the following exceptions. Using ratios, Badham (1976) described sexual dimorphism in adult tail length. Witten (1985) used allometric coefficients to investigate phylogeny in the Agamidae, but did not consider sex differences. Witten (1994) also analysed sexual dimorphism in other *Pogona* species. To address these issues in *P. barbata*, and to explore the possibility that environmental factors may influence growth related changes, we investigated allometry and sexual dimorphism within the species and among animals from three climate zones.

**Figure 1** Adult *Pogona barbata* basking on a log (Moonbi Ranges, NSW)(Photo: A. Stauber).

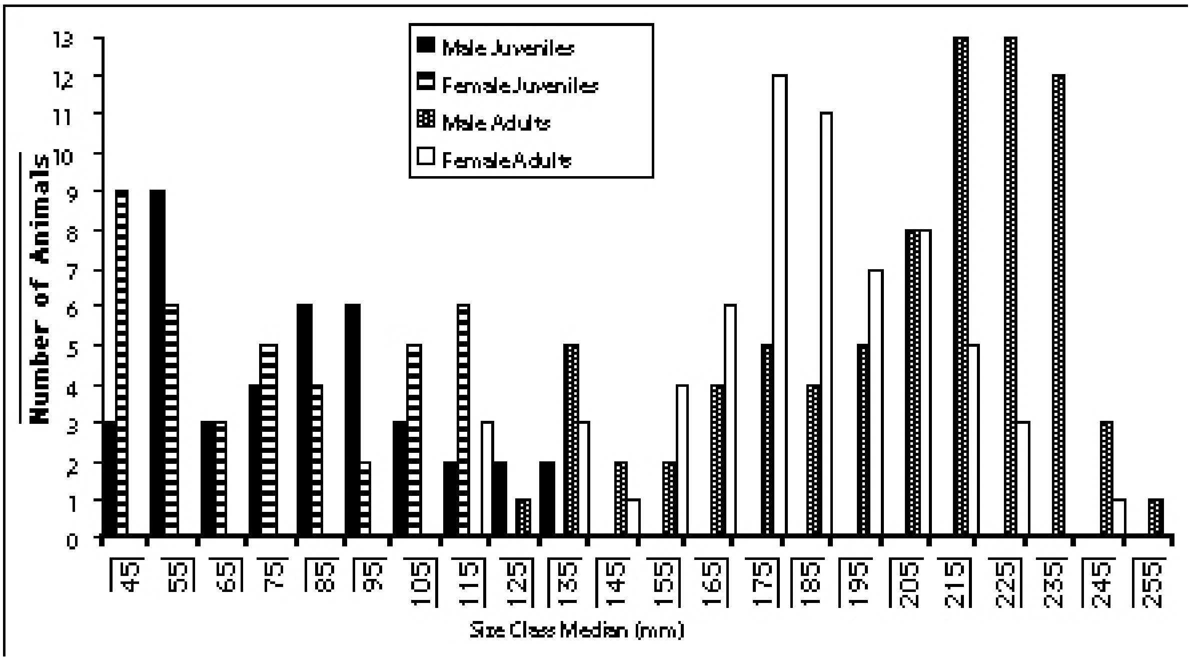

**Figure 3** Size class distribution of male and female *Pogona barbata* museum specimens (size class range = 10 mm).

## Materials and methods

### Biology of the Eastern Bearded Dragon *Pogona barbata*

*Pogona barbata* of the family Agamidae (Sauria) is a conspicuous lizard of variable colour with a maximum snout-vent length of 25 cm (Figure 1) (Badham 1976). The head and body are heavily built and depressed, and the body is covered in keeled scales of two distinct sizes. The distensible throat is covered in enlarged, often dark spines, and gives the species its common name. The species occurs in the east of the Australian mainland excluding Cape York Peninsula and most of Victoria. The lizard is semi-arboreal and often basks on top of stumps and fence posts (Cogger 1994). Food items include insects and flowers (Cogger 1994). The species is oviparous and females dig burrows in which they lay 15 - 31 eggs (Greer 1989). Social behaviour (Brattstrom 1971) and temperature regulation by physiological (Bartholomew and Tucker 1963), and behavioural means (Lee and Badham 1963; Bradshaw and Main 1968) are well documented.

### Museum Specimens Examined

The entire collection of preserved *P. barbata* specimens at the Australian Museum in Sydney, Australia, was inspected. We took data from all the animals that could be reliably measured and sexed, and whose identity was unambiguous (n = 236).

### Morphometric Measurements

Four measurements were recorded. 1) Head lengths (HL: tip of snout to lateral tip of extra-collumela) were recorded to 0.1 mm using dial callipers. 2) Snout-vent lengths (SVL) and 3) tail lengths (TL) were measured by pressing the animal against a 30 cm bench-mounted metal ruler. Animals with signs of broken tails were excluded. A second metal ruler was mounted perpendicularly to the edge of the bench, the zero mark in line with the edge. 4) Hind leg lengths (LL) were obtained by holding the animal upright and by pressing the base of the tail against the edge of the bench. The hind leg was then gently stretched along the ruler and the distance to the base of the claw on the fourth toe was recorded. Measurements obtained by ruler were estimated to the nearest 0.5 mm.

### Maturity and Sex Determination

Sex and state of maturity were determined by inspecting the gonads through a short lateral incision along the posterior flank. A binocular dissecting microscope was used to inspect small specimens. Males were classed as sexually mature if they had thick convoluted efferent ducts, or large, turgid testes; and females were rated as mature if they had thick oviducts, contained eggs or had ovarian follicles > 5 mm diameter (Witten and Coventry 1990).

## Geographic Location of Specimens and Separation of Animal Groups

To investigate possible links between climate and morphometrics, we identified three regional groups along the east-west rainfall gradient using all New South Wales (NSW) specimens. Average annual rainfall isohyets (Bureau of Meteorology 1995) were used as separators. The western group (W) included all animals west of the 600 mm isohyet, the eastern group (E) included all animals east of the 800 mm isohyet, and the central group was made up of all animals in between (Figure 2).

## Data Analyses

Mann-Whitney tests were applied to compare absolute measurements (SVL, TL, HL, LL) between the sexes. Allometric coefficients were calculated using reduced major axis regressions. While Model II regressions (Zar 1996) are preferred when a functional relationship is to be estimated (Fairbairn 1997), this study presents Model I results to facilitate comparison with other published data. This choice was justified by the high $r^2$ values obtained in most cases. All values quoted are components of the linear equivalent of Huxley's (1932) formula: $\ln y = \ln a + b \ln x$; where x is always snout-vent length (SVL), y is the size of the differentially growing organ (such as tail length) and b is the allometric coefficient. The intercept a is generally regarded as biologically meaningless (see Gould 1966). In this paper, all values except b are expressed as the equivalent of their natural logarithms (ln). Two-tailed t-tests were applied to test for allometry by comparing allometric coefficients to the isometric coefficient of one (Zar 1996). Juveniles and adults were analysed separately.

In order to test for sexual shape dimorphism, homogeneity of slopes was tested using General Linear Models (GLMs), and where appropriate, intercepts were compared using Analyses of Covariance (ANCOVA) (SYSTAT 1996). The factor in the models was sex and the covariate was ln SVL.

Sexual dimorphism was investigated within and among three different NSW regions to explore geographic differences. Adult SVLs were compared among regions and sexes using Mann-Whitney and Kruskal-Wallis tests. To investigate interactions between factors, sexual dimorphism was analysed with two-factor ANOVA and two-factor ANCOVA (factors: sex, region, covariate where applicable: ln SVL). To allow comparison of body shape among the three regional groups and among both sexes, GLMs and ANCOVAs were utilised in the same way as described in the previous section.

**Table 1** Sizes, sexual size dimorphism statistics and model I regression coefficients for 3 body parts in *Pogona barbata,* compared to snout-vent length. The coefficients a and b are components of Huxley's (1932) formula. Significance at the allometric coefficient b indicates that the relationship is not isometric ($b \neq 1$); n is the sample size. Adjusted $r^2$ values are given; significance is indicated as *** (99% confidence level).

| Body Part | | Median Length (mm) | | Sexual Size Dimorphism | | Model I Regression (sexes combined) (x = ln SVL) | | |
|---|---|---|---|---|---|---|---|---|
| | n | Males | Females | U statistic | p | $r^2$ | ln a±S.E. | b ± S.E. |
| SVL | 236 | 179.3 | 163.0 | 14356 | <0.003*** | - | - | - |
| Head | 233 | 242.3 | 238.0 | 14130 | <0.001*** | 0.99 | -0.64±0.02 | 0.85±0.01*** |
| Leg | 221 | 292.5 | 281.0 | 13685 | <0.001*** | 0.99 | -0.06±0.03 | 0.88±0.01*** |
| Tail | 232 | 241.0 | 208.8 | 14134 | <0.001*** | 0.98 | -0.45±0.04 | 0.97±0.01*** |

**Table 2** Model I regression coefficients for head, leg and tail lengths in *Pogona barbata* juveniles and adults, compared to snout-vent length. The coefficients a and b are components of Huxley's (1932) formula. Significance at the allometric coefficient b indicates that the relationship is not isometric ($b \neq 1$); n is sample size. Adjusted $r^2$ values are given; significance is indicated as *** (99% confidence level) and ** (95% confidence level).

| Sex | Size Class | Body Part (y) | n | $r^2$ | ln a±S.E. | b±S.E. |
|---|---|---|---|---|---|---|
| **Males** | Juveniles | Head | 40 | 0.99 | -0.62±0.1 | 0.84±0.02*** |
| | Adults | Head | 76 | 0.95 | -0.88±0.1 | 0.90±0.02*** |
| | Juveniles | Leg | 40 | 0.97 | -0.25±0.1 | 0.92±0.03*** |
| | Adults | Leg | 74 | 0.92 | 0.29±0.2 | 0.82±0.03*** |
| | Juveniles | Tail | 40 | 0.98 | -0.06±0.1 | 1.09±0.03*** |
| | Adults | Tail | 76 | 0.91 | 1.25±0.2 | 0.81±0.03*** |
| **Females** | Juveniles | Head | 40 | 0.99 | -0.57±0.1 | 0.82±0.01*** |
| | Adults | Head | 63 | 0.92 | -0.58±0.2 | 0.83±0.03*** |
| | Juveniles | Leg | 40 | 0.99 | -0.01±0.7 | 0.86±0.02*** |
| | Adults | Leg | 62 | 0.82 | 0.52±0.4 | 0.77±0.05*** |
| | Juveniles | Tail | 40 | 0.97 | -0.15±0.1 | 1.11±0.03*** |
| | Adults | Tail | 63 | 0.85 | 1.37±0.2 | 0.78±0.04*** |

# Results

## Sexual Size Dimorphism, Size at Maturity and Sex Ratios

Mean male SVL was 161±6.0 (S.E., n=118) mm, ranging from 42-255 mm, and maturity was attained between 127.5 mm and 135.5 mm SVL. In females, mean SVL was 142±5.9 (n=101) mm, ranging from 41-249 mm, and maturity was attained between 110.5 mm and 119.5 mm SVL. Size class distribution (Figure 3) and statistical analyses revealed that males were the larger sex and that all their measured body parts grew longer than in females (medians in Table 1). Overall, 50% of juveniles were males (40 males : 40 females), and 55% of adults were males (78 males : 64 females). Sex ratios did not significantly differ from a 1:1 ratio in both juveniles (exactly 1:1) and adults ($\chi^2_1 = 1.38$; $p > 0.05$).

## Allometry and Sexual Shape Dimorphism

The Model I regression values for the species are presented in Table 1. Head, leg and tail lengths were in negative allometry relative to snout-vent length; that is, the three body parts became relatively smaller with increasing body length.

Allometry for head length was negative in juveniles and adults of both sexes. However, the allometric coefficient for head length in adult males was significantly higher than in juveniles (Table 2). Mean juvenile head length was the same in both sexes, but adult males had relatively longer heads than mature females (Table 3). Allometry for leg length was negative in juveniles and adults of both sexes (Table 2). Sexual dimorphism in leg length became evident after maturity, with male limbs being longer (Table 3). A change in tail allometry coincided with the onset of maturity: tail length was in positive allometry in juveniles, but was in negative allometry in adults (Table 2). Sexual dimorphism in tail length occurred in adults only, with tails of males being relatively longer (Table 3). Over the whole range of sizes, sexual dimorphism was seen in all three measurements (Table 3). Males had relatively longer heads, legs and tails.

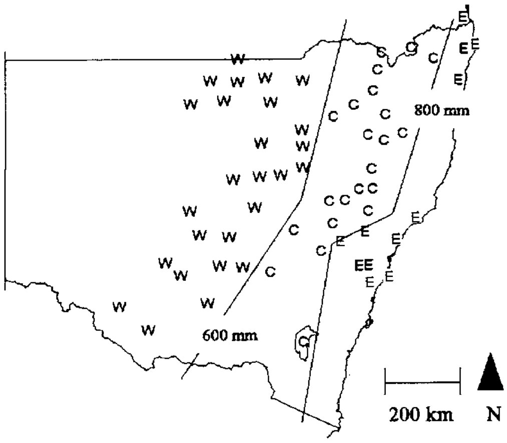

**Figure 2** Three NSW groups of *Pogona barbata* as defined by the local rainfall pattern. Letters indicate the locations of specimens and indicate membership of western (W), central (C) and eastern (E) group. The grey lines roughly follow the 600 and 800 mm rainfall isohyets.

## Sexual Dimorphism and Allometry in Three Regional Groups

One hundred and eighty four animals from NSW in the collection were considered suitable for examination. The size range of males and females were similar in each group. Two-factor ANOVA and ANCOVA suggested that there was no significant sex by region interaction on each length measurement (lnSVL: F = 0.07, d.f. = 2, p = 0.93; lnHL: F = 1.67, d.f. = 2, p = 0.19; lnLL: F = 1.18, d.f. = 2, p = 0.31; lnTL: F = 0.71, d.f. = 2, p = 0.50). Adult males were significantly larger in each regional group (west: U = 663, p = 0.001; centre: U = 231, p = 0.019; east: U = 800, p = 0.008). Western adult males were significantly larger than males elsewhere (H = 6.22, d.f. = 2, p = 0.045) while SVLs of females were similar among regions(H = 3.24, d.f. = 2, p = 0.198). Median adult sizes are shown in Table 4.

In the absence of significant sex by region interactions, each group was analysed consistent with the previous analyses of the animals across their full distribution range. In the western group, heads and legs were proportionately longer in males than in females, no dimorphism was

**Table 3** Sexual shape dimorphism in *Pogona barbata*. Analyses of covariance were carried out over the whole range of sizes (All), and juveniles and adults separately. The covariate is snout-vent length (ln transformed). a and b are components of Huxley's (1932) formula. Significance is indicated as *** (99% confidence level).

| Size Class | Body Part | | Comparison of slopes (b) | | Comparison of elevations (ln a) | |
|---|---|---|---|---|---|---|
| | | n | F-statistic | p | F-statistic | p |
| All | Head | 216 | 20.09 | 0.000*** | 2- | 2- |
| | Leg | 209 | 23.08 | 0.081 | 26.91 | 20.009*** |
| | Tail | 216 | 20.20 | 0.655 | 10.22 | 20.002*** |
| Juveniles | Head | 280 | 20.62 | 0.433 | 23.07 | 20.084 |
| | Leg | 280 | 23.42 | 0.068 | 21.36 | 20.248 |
| | Tail | 280 | 20.16 | 0.693 | 20.76 | 20.387 |
| Adults | Head | 139 | 23.33 | 0.070 | 56.25 | <0.001*** |
| | Leg | 136 | 20.97 | 0.330 | 14.02 | <0.001*** |
| | Tail | 139 | 20.42 | 0.520 | 25.71 | <0.001*** |

**Table 4** Adult sizes of *Pogona barbata* for each sex in three NSW groups.

| Animal Group | n | median SVL (mm) |
|---|---|---|
| West Males | 24 | 221 |
| West Females | 19 | 184 |
| Centre Males | 13 | 211 |
| Centre Females | 14 | 178 |
| East Males | 26 | 214 |
| East Females | 24 | 189 |

evident in tail length (Table 5). The central group showed no sexual shape dimorphism in head, leg and tail lengths. Males in the east had longer heads and tails, but leg lengths were similar between the sexes. Except for tail proportions in most cases, regression coefficients showed negative allometry in each tested relationship (Table 6).

## Regional Group Differences within Males and Females

Group differences within the sexes are summarised in Table 5 (regression coefficients in Table 6). Heads were proportionately smaller in western males, but of similar size in males of the central and eastern group. Relative leg length did not differ between the western and central groups, but eastern males had proportionately longer legs than males in the other groups. In males, relative tail length was similar among the three groups. Western females had proportionately smaller heads than eastern females and relative head size of the central group did not differ in comparison to females of the other groups. The legs were shortest in the western females, and of equal length in the centre and east. In females, tail length was similar between the three groups.

**Table 5** Shape dimorphism among and within sexes in three NSW *Pogona barbata* regional groups. Analyses are one-factor ANCOVAs, where the covariate is snout-vent length (ln transformed). a and b are components of Huxley's (1932) formula. Significance is indicated as *** (99% confidence level) and ** (95% confidence level).

| Group | Body Part | | Comparison of slopes (b) | | Comparison of elevations (ln a) | |
|---|---|---|---|---|---|---|
| | | n | F-statistic | p | F-statistic | p |
| West | Head | 50 | 1.57 | 0.217 | 14.06 | 0.005*** |
| | Leg | 49 | 0.95 | 0.334 | 26.32 | 0.015** |
| | Tail | 51 | 0.07 | 0.792 | 21.42 | 0.240 |
| Centre | Head | 53 | 0.30 | 0.588 | 11.61 | 0.210 |
| | Leg | 53 | 0.43 | 0.512 | 10.06 | 0.810 |
| | Tail | 52 | 0.02 | 0.894 | 10.34 | 0.560 |
| East | Head | 79 | 9.02 | 0.004*** | - | - |
| | Leg | 76 | 0.27 | 0.604 | 11.20 | 0.276 |
| | Tail | 77 | 0.04 | 0.840 | 18.62 | 0.004*** |
| Males | Head | 92 | 2.03 | 0.138 | 14.90 | 0.010** |
| | Leg | 90 | 0.33 | 0.717 | 10.04 | <0.001*** |
| | Tail | 92 | 2.34 | 0.103 | 11.50 | <0.228 |
| Females | Head | 89 | 1.78 | 0.175 | 14.73 | 0.011** |
| | Leg | 88 | 0.79 | 0.459 | 10.65 | <0.001*** |
| | Tail | 89 | 0.49 | 0.612 | 10.49 | <0.617 |

**Table 6** Summary of model I regression analyses for male and female *Pogona barbata* from three different NSW regions. The coefficients a and b are components of Huxley's (1932) formula. The independent variable is snout-vent length (ln transformed); n is sample size. Significance at the allometric coefficient b indicates that the relationship is not isometric ($b \neq 1$). Adjusted $r^2$ values are given; significance is indicated as *** (99% confidence level).

| Group | Body Part | | | Males | | | | Females | |
|---|---|---|---|---|---|---|---|---|---|
| | y | n | $r^2$ | ln a±S.E. | b±S.E. | n | $r^2$ | ln a±S.E. | b±S.E. |
| West | Head | 26 | 21.0 | -0.83±0.1 | 0.88±0.01*** | 24 | 0.99 | -0.72±0.1 | 0.85±0.02*** |
| | Leg | 25 | 0.99 | -0.14±0.1 | 0.89±0.01*** | 24 | 0.98 | -0.03±0.1 | 0.86±0.03*** |
| | Tail | 27 | 0.99 | -0.70±0.1 | 0.92±0.02*** | 24 | 0.95 | -0.62±0.2 | 0.93±0.04 |
| Centre | Head | 24 | 0.99 | -0.78±0.1 | 0.88±0.02*** | 28 | 1.0 | -0.60±0.1 | 0.83±0.01*** |
| | Leg | 24 | 0.99 | -0.12±0.1 | 0.89±0.02*** | 29 | 0.99 | -0.05±0.1 | 0.88±0.02*** |
| | Tail | 24 | 0.99 | -0.45±0.1 | 0.97±0.02 | 29 | 0.97 | -0.47±0.1 | 0.96±0.03 |
| East | Head | 42 | 21.0 | -0.66±0.0 | 0.85±0.01*** | 37 | 1.0 | -0.52±0.0 | 0.82±0.01*** |
| | Leg | 41 | 0.99 | -0.17±0.1 | 0.91±0.01*** | 35 | 0.99 | -0.13±0.1 | 0.90±0.01*** |
| | Tail | 41 | 0.99 | -0.40±0.1 | 0.98±0.01 | 36 | 0.99 | -0.39±0.1 | 0.98±0.02 |

# Discussion

## Size at Maturity and Sex Ratios

In *P. barbata*, males matured at larger body sizes (mean SVL = 131.5 mm) than did females (mean SVL = 115.0 mm). In light of our results, the SVL of 95 mm of a single mature male *P. barbata* by Witten and Coventry (1990) appears exceptionally short. Badham (1976) classed *P. barbata* males and females with a SVL of less than 130 mm as juveniles, and stated that females reach sexual maturity at 130 mm SVL. It is not clear from her publication how the author arrived at such a conclusion. While size at maturity in males was consistent with Badham's (1976) statement, we found it not applicable to females.

## Sexual Size Dimorphism

Badham (1976) reported that male *P. barbata* attain longer SVLs than females, however the present study provides a more detailed examination of sexual dimorphism in the species. Adult *P. barbata* males were larger than females and had proportionately larger heads, legs and tails. It appears that sexual size dimorphism in *P. barbata* is, at least in part, achieved by males maturing at a larger size.

Our results contrast with the general trend for larger females among amphibians and reptiles (Fairbairn 1997). While the direction of sexual size dimorphism may be consistent within some broad phylogenetic groups (Shine 1978; Fitch 1981) these results and data collated by Greer (1989) suggest that such a generalisation may not hold for the family of Agamidae.

Differentiation of reproductive roles, differences in parental investment and the relationship between mating frequency and reproductive success (Fairbairn 1997) can lead to sexual dimorphism. Strong intrasexual selection on males can also be the primary selective advantage responsible for dimorphism (Shine 1994). Sexual size differences could also be influenced by age structure of a population. Growth in reptiles is continuous (Shine and Charnov 1992), therefore the situation where males live longer than females could produce a population in which males are the larger sex. Alternatively, different growth rates between the sexes could produce differences in adult sizes. Egg production may result in slower growth in females. Possible causes underlying size dimorphism in *P. barbata* could be tested by ageing individuals and obtaining growth rates of wild populations.

## Allometry and Sexual Shape Dimorphism

Juvenile *P. barbata* had relatively longer heads, legs and tails than adults. Allometric rates seemingly corresponded to absolute size of the part under consideration, thus the allometric coefficient was lowest for head length, followed by leg length, and allometry in tail length was highest. Witten (1985) obtained similar results for leg and tail lengths of *P. barbata* and *P. vitticeps*.

Negative allometry of the head as observed in *P. barbata* is common among *Pogona* (Witten 1994), and indeed most other vertebrates (Rensch 1960). Reflecting the pattern observed in *P. vitticeps* (Witten 1994), allometry in head size was higher in adult male *P. barbata* than in juveniles. Similar results were found in Frillneck Lizards *Chlamydosaurus kingii*, where allometry in jaw length increases in large adults (Christian *et al.* 1995). The increased allometric rate for head size was not observed in adult females, and is thus considered one of the factors responsible for sexual dimorphism.

Larger head sizes in males was also reported for other congeners (Witten 1994). Analysis of prey item sizes in juveniles and adults of both genders would show whether the allometric pattern is related to ecological niche diversification. Alternatively or in addition, intrasexual social behaviour may favour larger heads in males, but it remains unknown whether intrasexual social behaviour is equally important in females. As Kästle (1966) pointed out, antagonistic social behaviour in agamids can vary greatly between the sexes.

Allometry for leg length in *P. barbata* was negative in both juveniles and adults, however in adults, males had proportionately longer legs than females. These results reflect those obtained from other *Pogona* (Witten 1994), and support the claim that negative allometry in hind leg growth is the norm amongst most species of Australian agamids (Witten 1985). Leg allometry in lizards is influenced by two contrasting factors. The sprawling limb posture leads to long outlevers, requiring more muscle force to keep joints in equilibrium, unless the limbs are short (Christian and Garland 1996). Consequently, size-related decreases in leg length could be expected with increasing body size. However, shorter limbs affect sprinting and jumping ability (Christian and Garland 1996). We suspect that juvenile *P. barbata*, lacking spines and effective displays, rely on fleeing to avert danger, whereas spines and adult behaviours such as "freezing" when threatened with beard extended (Greer 1989), seem to fit the allometric pattern where running ability becomes relatively less important as animal size increases.

Allometry for tail length in juveniles was positive, whereas in adults it was negative. Similarly a change in the direction of tail allometry coinciding with the onset of maturity also occurs in *P. minor* (Witten 1994). It is not unusual that breaks in allometric patterns occur with maturity (see Gould 1966 for other examples). Tail allometry in *Pogona* is not strong but variable. Witten (1994) placed *P. barbata* within an intermediate group together with *P. vitticeps* and *P. nullarbor.* Greer (1989) suggested that tails may serve to counterbalance body weight in active agamids, but these active species have relatively much longer tails than the sedentary *P. barbata*. Negative allometry in tail length may thus again reflect the species' reliance on defence posture (Brattstrom 1971) and "freezing" (Greer 1989) rather than running from danger.

Sexual dimorphism in tail length was expressed in adults only, with males having relatively longer tails. The adaptive significance of these findings is not clear, but it is possible that a longer tail in males serves to counterbalance the bigger head, or to accommodate the hemipenes.

## Geographic Variation

Males were the larger sex within each region, and males were largest in the West. Allometries for head and leg length were negative whereas tail proportions generally remained constant in each of the three regions. Males in western NSW had larger heads and longer legs than females in the same region, whereas eastern males had larger heads and longer tails than females, and central animals showed no sexual dimorphism in head, leg and tail length.

Using ratios, Badham (1976) reported that females from a small area, constituting part of the western group in this report, had relatively shorter tails than males. This is contrary to the results obtained in our study for this particular group, where relative tail length did not vary among the sexes. Tail growth in western females, however, showed greater variability than measurements from the other regions.

Within-sex comparisons revealed that relative head and leg length decreased in both sexes with increasing distance from the coast. Within each sex, relative tail lengths did not vary among the regions.

Apart from rainfall, regional variation may be related to food type and availability, predation, population density and other climatic factors. At least some of the observed geographic variation may reflect ecological niche diversification. Geographic variation in head size in *Anolis* lizards (Schoener 1967) is related to the size of prey items. The influence of environmental differences on leg length requires further studies. Unexplained geographic variation in sexual dimorphism also occurs in *C. kingii* (Christian *et al.* 1995).

The ecological and evolutionary significance of sexual dimorphism and geographic variation in *P. barbata* remain obscure. We suggest that a combination of genetic drift and phenotypic responses are likely causes of these variations. It remains to be seen whether the observed allometric patterns are due to functional relationships or phylogenetic conservatism.

These geographic differences highlight a problem that arises when attempting to generalise allometry and sexual dimorphism for a species from limited samples. Some doubts arise about the suitability of allometry in phylogeny, as extensive sampling would be required across a species range. Allometry however can be a useful, even predictive tool, in population studies, and appropriately scaled community and ecosystem studies (eg. Cyr and Pace 1993).

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## References

**Badham, J.A. 1976**. The *Amphibolurus barbatus* species-group (Lacertilia: Agamidae). *Australian Journal of Zoology* **24**: 423-43.

**Bartholomew, G.A. and Tucker, V.A. 1963**. Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiological Zoology* **36**: 199-218.

**Bradshaw, S.D. and Main, A.R. 1968**. Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *Journal of Zoology (London)* **154**: 193-221.

**Brattstrom, B.H. 1971**. Social and thermoregulatory behaviour of the bearded dragon, *Amphibolurus barbatus*. *Copeia* **1971**: 484-97.

**Bureau of Meteorology. 1995**. *Average Annual Rainfall, NSW.* Prepared by Climate and Consultancy, Bureau of Meteorology, NSW.

**Christian, A. and Garland, T. 1996**. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). *Journal of Herpetology* **30**: 219-30.

**Christian, K., Bedford, G. and Griffiths, A. 1995**. Frillneck lizard morphology: comparisons between sexes and sites. *Journal of Herpetology* **29**: 576-83.

**Cogger, H.G. 1994**. *Reptiles and Amphibians of Australia.* 5th Edition. Reed, Sydney.

**Cuvier, G.L.C.F.D. 1829**. *Le regne animal.* 2nd Edition. Volume 2, Deterville, Paris.

**Cyr, H. and Pace, M.L. 1993**. Allometric theory: extrapolations from individuals to communities. *Ecology* **74**: 1234-45.

**Fairbairn, D.J. 1997**. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**: 659-87.

**Fitch, H.S. 1981**. Sexual size differences in reptiles. *Miscellaneous Publications. University of Kansas Museum of Natural History* **70**: 1-72.

**Gould, S.J. 1966**. Allometry and size in ontogeny and phylogeny. *Biological Reviews. Cambridge Philosophical Society* **41**: 587-640.

**Greer, A.E. 1989**. *The Biology and Ecology of Australian Lizards.* Surrey Beatty & Sons, Sydney.

**Huxley, J.S. 1932**. *Problems of Relative Growth.* Methuen, London.

**Kästle, W. 1966**. Beobachtungen an ceylonischen Taubagamen. *Salamandra* **2**: 78-87.

**Lee, A.K. and Badham, J.A. 1963**. Body temperature, activity, and behaviour of the agamid lizard, *Amphibolurus barbatus*. *Copeia* **1963**: 387-94.

**Patchell, F.C. and Shine, R. 1986**. Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). *Copeia* **1986**: 30-9.

**Rensch, B. 1960**. *Evolution Above the Species Level.* Columbia

University Press, New York.

**Schoener, T.W. 1967**. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**: 474-76.

**Shine, R. 1978**. Sexual size dimorphism and male combat in snakes. *Oecologia* **33**: 269-77.

**Shine, R. 1994**. Sexual size dimorphism in snakes revisited. *Copeia* **1994**: 326-46.

**Shine, R. and Charnov, E.L. 1992**. Patterns of survival, growth, and maturation in snakes and lizards. *American Naturalist* **139**: 1257-69.

**Shine, R., Harlow, P.S., Keogh, J.S. and Boeadi. 1998**. The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*). *Journal of Zoology (London)* **244**: 405-14.

**SYSTAT. 1996**. *SYSTAT 6.0 for Windows: Statistics.* SPSS Inc., Chicago.

**Weatherly, A.H. and Gill, H.S. 1987**. *The Biology of Fish Growth.* Academic Press, London.

**Webb, G.J.W. and Messel, H. 1978**. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, Northern Australia. *Australian Journal of Zoology* **26**: 1-27.

**Witten, G.J. 1985**. Relative growth in Australian Agamid lizards: Adaptation and evolution. *Australian Journal of Zoology* **33**: 349-62.

**Witten, G.J. 1994**. Relative growth in *Pogona* (Reptilia: Lacertilia: Agamidae). *Memoirs. Queensland Museum* **37**: 345-56.

**Witten, G.J. and Coventry, A.J. 1990**. Small *Pogona vitticeps* (Reptilia: Agamidae) from the Big Desert, Victoria, with notes on other *Pogona* populations. *Proceedings. Royal Society of Victoria* **102**: 117-20.

**Zar, J.H. 1996**. *Biostatistical Analysis.* 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey.